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**Climate-mediated changes in marine ecosystem regulation during El Niño**

Running title: Climate change and ecosystem regulation

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## 19    **Abstract**

20    The degree to which ecosystems are regulated through bottom-up, top-down or direct physical  
21    processes represents a long-standing issue in ecology, with important consequences for resource  
22    management and conservation. In marine ecosystems, the role of bottom-up and top-down  
23    forcing has been shown to vary over spatio-temporal scales, often linked to highly variable and  
24    heterogeneously distributed environmental conditions. Ecosystem dynamics in the Northeast  
25    Pacific have been suggested to be predominately bottom-up regulated. However, it remains  
26    unknown to what extent top-down regulation occurs, or whether the relative importance of  
27    bottom-up and top-down forcing may shift in response to climate change. In this study, we  
28    investigate the effects and relative importance of bottom-up, top-down and physical forcing  
29    during changing climate conditions on ecosystem regulation in the Southern California Current  
30    System (SCCS) using a generalized food web model. This statistical approach is based on non-  
31    linear threshold models and a long-term data set (~60 year) covering multiple trophic levels from  
32    phytoplankton to predatory fish. We found bottom-up control to be the primary mode of  
33    ecosystem regulation. However, our results also demonstrate an alternative mode of regulation  
34    represented by interacting bottom-up and top-down forcing, analogous to wasp-waist dynamics,  
35    but occurring across multiple trophic levels and only during periods of reduced bottom-up  
36    forcing (i.e., weak upwelling, low nutrient concentrations and primary production). The shifts in  
37    ecosystem regulation are caused by changes in ocean-atmosphere forcing and triggered by highly  
38    variable climate conditions associated with El Niño. Furthermore, we show that biota respond  
39    differently to major El Niño events during positive or negative phases of the Pacific Decadal  
40    Oscillation (PDO), as well as highlight potential concerns for marine and fisheries management  
41    by demonstrating increased sensitivity of pelagic fish to exploitation during El Niño.

**Introduction**

The degree to which terrestrial and aquatic ecosystems are regulated through bottom-up (resource-driven), top-down (consumer-driven) or direct physical (climate-driven) processes represents a long-standing issue in ecology (Power 1992; Strong 1992; Polis *et al.*, 2000; Worm & Myers 2003; Strong & Frank 2010), with important consequences for resource management and conservation (Cury *et al.*, 2003; Llope *et al.*, 2011; Blenckner *et al.*, 2015; Lynam *et al.*, 2017). Although it is presently recognized that these processes are not mutually exclusive, the conditions under which one of these processes dominate and whether climate change can trigger changes in their relative importance remain largely unknown. In marine ecosystems, the role of bottom-up and top-down forcing has been shown to vary with latitude, where the former dominates in areas with high temperature and species richness and vice versa (Frank *et al.*, 2007; Boyce *et al.*, 2015). Upwelling areas, such as the Humboldt and Benguela Currents, have been hypothesized to represent “wasp-waist” ecosystems, where mid-trophic levels dominated by a few species of planktivorous fish (e.g., sardine and anchovy), may exert both top-down control on their prey and bottom-up control on their predators (Rice 1995; Cury *et al.*, 2000, 2003) (Fig. 1). However, direct physical processes, such as related to transport and advection of nutrients and organisms may also predominate in upwelling systems, including the California Current (Parrish *et al.*, 1981; Brinton & Townsend 2003; Koslow *et al.*, 2014).

The relative importance of bottom-up and top-down forcing has been shown to vary over spatio-temporal scales, often linked to highly variable environmental conditions (Polis *et al.*, 1997; Hunt & McKinnell 2006; Litzow & Ciannelli 2007; Lindegren *et al.*, 2012), as well as the degree

of spatial connectivity between areas (Casini *et al.*, 2012). For instance, ecosystem dynamics in the Eastern Bering Sea have been shown to alternate between bottom-up and top-down control during cold and warm regimes, caused by decadal variability in temperature affecting the timing of the spring bloom, the composition of the zooplankton community and recruitment of key fish species, e.g., walleye Pollock (*Theragra chalcogramma*) (Coyle *et al.*, 2011; Hunt *et al.*, 2011). Similar alteration between bottom-up and top-down regulation has also been suggested to occur in wasp-waist ecosystems, where during periods of high abundances mid-trophic level species may instead exert top-down control on their predators, either through direct predation or via food competition with early life-stages of their predators (Bakun 2006).

The El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) represent two major modes of climate variability across the tropical and North Pacific, affecting a suite of abiotic and biotic conditions related to temperature, transport, nutrient availability and productivity (Bjerknes 1966; Chelton *et al.*, 1982; Mantua *et al.*, 1997; Chavez *et al.*, 2002). While the effects of ENSO events, i.e., El Niño (anomalously warm) and La Niña (anomalously cold), are short-lived and occur at relatively high frequencies (Philander & Federov 2003), positive and negative phases of the PDO may persist for decades with long-lasting consequences for the biota (Mantua *et al.*, 1997; Minobe 1997). Furthermore, phase transitions in the PDO may coincide with changes in the relative frequency of ENSO events, i.e., enhanced frequency of El Niño during positive phases of the PDO and vice versa (Verdon & Franks 2006). Although not studied in detail, it is suggested that potential phase differences between the ENSO and PDO may serve to weaken or strengthen the effect of El Niño and La Niña events on the biota (Chelton *et al.*, 1982; Chavez *et al.*, 2002). Despite pronounced climate variability, ecosystem

dynamics in the Northeast Pacific, including a wide range of open marine ecosystems from southern California to Alaska, have been suggested to be predominately bottom-up regulated (Ware & Thompson 2005). However, it remains unknown to what extent top-down forcing can exert a regulatory role, or whether the relative importance of bottom-up, top-down or direct physical forcing may change in response to climate variability and future climate change.

The Southern California Current System (SCCS) is a highly productive ecosystem strongly impacted by climate variability across a range of spatial and temporal scales (Rykaczewski & Checkley 2008; Checkley & Barth 2009; DiLorenzo and Ohman 2013). This is largely due to its geographical location and interactions of both a high-frequency tropical and low-frequency temperate mode of climate variability, caused by ENSO and PDO, respectively (Lluch-Cota *et al.*, 2003). Likewise, biotic variables of the SCCS display pronounced variability ranging from inter-annual to multi-decadal fluctuations of e.g., meso- and macrozooplankton, marine mammals and birds, as well as mesopelagic and pelagic fish (Rebstock 2002; Brinton & Townsend 2003; Smith & Moser 2003; Sydeman *et al.*, 2009; Koslow *et al.*, 2011). These include non-target and commercially important prey and predatory fish species, such as sardine (*Sardinops sagax*), anchovy (*Engraulis mordax*) and Pacific hake (*Merluccius productus*). Although climate effects on population dynamics of single, or groups of species have been extensively studied (Lavaniegos & Ohman 2007; Rykaczewski & Checkley 2008; Koslow *et al.*, 2011, 2013, 2014; Lindegren & Checkley 2013; Lindegren *et al.*, 2013; DiLorenzo & Ohman 2013), little is known regarding the combined effects of bottom-up, top-down and direct physical forcing on the food web dynamics across multiple trophic levels. In this study, we investigate the effects and relative importance of bottom-up and top-down forcing on the food web

dynamics of the SCCS during changing climate conditions using a generalized food web model. The generalized model represents links between several functional groups and trophic levels but does not resolve interactions at the level of individual species. This statistical approach is based on non-linear threshold models, fitted and parameterized using a unique long-term data set (~60 year), largely based on the *California Cooperative Oceanic Fisheries Investigations* (CalCOFI) monitoring program, supplemented by the *California Current Ecosystem Long-Term Ecological Research* site, covering multiple trophic levels from phytoplankton to predatory fish. We show evidence of strong bottom-up regulation throughout the food web, interacting with moderate top-down forcing, but only during periods of unfavorable climate conditions primarily associated with certain combinations of ENSO and PDO. Furthermore, we elaborate on the effects of major El Niño events, if occurring during the positive or negative phase of the PDO, as well as demonstrate potential concerns for marine- and fisheries management in the face of climate change.

## Material and Methods

### 1.1 Data collection

An inventory of data characterising the ocean-atmospheric, hydrographic, physical and biotic conditions across multiple trophic levels in the SCCS over the time period from 1951 to 2010 was performed (Table S1). In order to reflect the ocean-atmospheric conditions affecting regional climate in the area, a number of large-scale climate indices, including the PDO (Mantua *et al.* 1997), the tropical Multivariate ENSO Index (MEI), the Southern Oscillation Index (SOI), as well as the North Pacific Gyre Oscillation (NPGO) (DiLorenzo *et al.*, 2008) were included.

To reflect the hydrodynamic conditions, coastal upwelling, open-ocean (wind stress curl-driven) upwelling (Rykaczewski & Checkley 2008), sea level height (detrended), alongshore (North-South) transport, as well as dynamic height were used. Physical conditions were represented by spring averages of 0-100 m temperature, salinity, water density ( $\sigma_t$ ) and oxygen concentration across all stations of the regular CalCOFI area (i.e., from line 76.7 to 93.3; Figure S1). Nutrient conditions were represented by average concentrations of nitrate in the mixed layer. Since nitrate was consistently sampled only from 1984 onwards, we extended its time series backwards until 1951 based on modelled estimates. These were derived from a Generalized Additive Model (GAM) with upwelling, temperature and sea level as predictors, demonstrating highly significant and temporally consistent relationships overall (Table S2; Figure S2, S4) and a high degree of explained deviance (79.4%). Finally, a set of biotic (response) variables representing separate trophic levels was compiled. The mean spring chlorophyll *a* in the mixed layer was chosen to characterize primary producers. Note that due to lack of chlorophyll *a* data prior to 1984 we extended the time series backwards until 1951 with modelled estimates (Table S2-S3; Figure S3), based on a GAM explaining a high degree of deviance from 1984-2010 (87.8%). The spring carbon biomass of mesozooplankton, excluding euphausiids, here termed ‘other zooplankton’ and euphausiids, the latter divided into a warm-water (subtropical) and cold-water (temperate) assemblage (Brinton & Townsend 2003), were used to represent intermediate trophic levels (see details in Lavaniegos & Ohman, 2007).

To represent key consumers of both meso- and macrozooplankton (euphausiids) and prey for higher trophic level predators, an aggregated index of mesopelagic fish abundance, derived from ichthyoplankton samples (Koslow *et al.*, 2011), as well as the total spawning stock biomass



(SSB) of small pelagic fish was used. The latter group consists of the dominant consumers of copepods and euphausiids including Pacific sardine, northern anchovy and Pacific mackerel (*Scomber japonicus*), respectively, for which comparable biomass estimates are available from stock assessments (Murphy 1966; Jacobson *et al.*, 1994; Fissel *et al.*, 2009; Hill *et al.*, 2011; Crone *et al.*, 2011). Note that, in the absence of sardine stock assessments during the period of low stock size from 1963 to 1980, hindcasted model estimates were used (Lindgren *et al.*, 2013). Finally, ichthyoplankton samples of Pacific hake, as well as stock assessment estimates of hake fishing mortality (Stewart & Forrest 2011) and albacore (*Thunnus alalunga*) catch-per-unit effort (CPUE) data (ALBWG 2011) were used to characterize the dominant predatory fish in the area (Figure S4). Because of its highly migratory behavior and transitory residence in the California Current, albacore was treated as an external covariate only. In addition to these predators, sharks, billfishes (e.g., striped marlin and swordfish), as well as marine birds and mammals constitute other top predators in the SCCE (Bedford & Hagerman 1983; Barlow *et al.*, 2008; Sydeman *et al.*, 2015). Unfortunately, the considerably shorter length of monitoring time series for these groups (e.g., 1987 and 1991 onwards for birds and cetaceans, respectively; Hyrenbach & Veit 2003; Barlow & Forney 2007), precludes a comparable long-term analysis of climate forcing and trophic interactions on these predators. Nevertheless, we will discuss our findings regarding climate effects and trophic regulation in the SCCE with reference also to these top predators.

## 1.2 Food web model setup and validation

In order to account for potential threshold-dependent relationships, we used a modified formulation of Generalized Additive Models, so-called threshold Generalized Additive Models

(TGAM), allowing for non-additive effects of the explanatory variables below and above a certain threshold value ( $\phi$ ) estimated from the data (Ciannelli *et al.*, 2004). Since our aim was to investigate whether bottom-up and top-down processes depend on climate, in particular the indirect or direct effects of ENSO and PDO on resource availability (Chelton *et al.*, 1982), we treated the PDO, MEI, total nitrate and chlorophyll *a* as candidate threshold variables and allowed the model to test for potential threshold values. For mesopelagic fish we treated deep-water oxygen (200-400m) as a potential threshold variable due to its proposed effect on habitat size and predator-prey overlap (Koslow *et al.*, 2011). In order to assess potential state-dependent relationships between small pelagic fish and predatory fish (Bakun 2006) we also tested an alternative model formulation where the biomass of small pelagic fish was used a threshold variable in the hake model. The following non-additive model formulation with  $\log(x+1)$  transformed biomass (or abundance) indices for each trophic level as response variables (*y*) was used:

$$y_{i,t} = a + \begin{cases} s(X_{i-1,t}) + s(X_{i+1,t}) + s(V_{1,t}) + \dots + s(V_{n,t}) + \varepsilon_t & \text{if } TV > \Phi \\ s(X_{i-1,t}) + s(X_{i+1,t}) + s(V_{1,t}) + \dots + s(V_{n,t}) + \varepsilon_t & \text{if } TV \leq \Phi \end{cases}$$

where *a* is the intercept, *s* the thin plate smoothing function (Wood 2003),  $x_{i,t}$  the biomass (or abundance) at time *t* for each trophic level *i* (i.e., where *i-1* and *i+1* represent direct predator-prey interactions between adjacent trophic levels occurring without time lags),  $v_1 \dots v_n$  a number of selected climate predictors known to affect the dynamics of each trophic level, TV the threshold variable, and  $\varepsilon$  the error term. We applied a stepwise backward selection routine based on the generalized cross validation criterion (GCV) and partial *F*-tests to find the best possible set of predictors for each trophic level model. Furthermore, the spline smoother function (*s*) was constrained to three degrees of freedom (*k*=3), in order to allow for potential nonlinearities but

restrict flexibility during model fitting. Finally, we tested whether the non-additive models proved significantly better than regular GAMs (fitted without thresholds) by comparing the genuine CV, i.e., the average squared leave-one-out prediction errors (Ciannelli *et al.*, 2004). To validate the predictive capabilities of the model, we hindcasted historical food web dynamics by dynamically coupling each separate trophic level model into a generalized food web model, where the internal dynamics (i.e., trophic interactions) are forced only by the external covariates (Llope *et al.*, 2011; Blenckner *et al.*, 2015; Lynam *et al.*, 2017). The food web model was initialised with the observed biomass (or abundance) values in 1966, the first year with available observations for all covariates (i.e., albacore data are missing prior to 1966), and run throughout the period until 2010 with observed covariate values. To account for uncertainty we added process noise, resampled from the residuals of each trophic level model, and performed 1000 replicated model runs. In order to retain any temporal dependence (correlation) between errors across trophic levels, an entire vector of errors corresponding to a randomly sampled set of model residuals for a given year was used. The hindcasted estimates were then compared with the actual observed values for each trophic level to validate the predictive accuracy of the food web model for the study period.

### *1.3 El Niño simulations and management scenarios*

In order to investigate the effect of major El Niño events and particularly whether phase differences between the ENSO and PDO may serve to weaken or strengthen the biotic response across trophic levels, we exposed the validated food web model to a simulated El Niño event, represented by the observed covariate values during the record strong El Niño in 1998 (Chavez

*et al.*, 2002). This pulse perturbation was introduced during both a negative and positive phase of the PDO, defined as the mean covariate values observed prior to and after the PDO phase shift in 1976-1977 (Mantua *et al.*, 1997). These simulations were initialized at the mean biomass (or abundance) for each trophic level and forced with the mean covariate values, both averaged during the negative and positive phases of the PDO, over a period of 10 years. Thereafter, the El Niño pulse perturbation was introduced and the relative difference in non-log biomass (or abundance) before and during the perturbation was estimated as a measure of the strength of the biotic response (e.g., a value <1 would indicate a decline) (Figure S6). Furthermore, we illustrated potential management implications by assessing the effect of exploitation on the commercially important small pelagic fishery during periods of low or high productivity, respectively. These were defined as periods of low and high nitrate availability, as occurring during positive and negative phases of MEI, and correspond to the mean covariate values above and below the estimated MEI threshold of 0.371 (Fig. S7i,j). The effect of exploitation was quantified as the change in total spawning stock biomass (SSB) relative to an equilibrium SSB (i.e., 0.77 and 0.44 million metric tonnes below and above the MEI threshold, respectively) when forced by a range of fishing mortalities ( $F$ ) from 0 to  $0.6\text{ y}^{-1}$  for a period of 10 years (i.e.,  $SSB_t = SSB_{t-1} * e(-F)$ ). All statistical analyses were conducted using the R software ([www.r-project.org](http://www.r-project.org)).

**Results**

All trophic level models demonstrate strongly significant interactions and a high degree of explained deviance (Table 1). The type of interactions range from linear to non-linear relationships, occurring with or without threshold-dependent dynamics and illustrate a combination of bottom-up and top-down effects and direct physical forcing throughout the

modelled food web (Fig. 2). We recognize that these statistical relationships do not necessarily reflect direct causation, but for convenience we refer to these as “effects” and provide references to known relationships documented in the literature. The bottom-up effects are shown as positive linear or curvilinear relationships, predominately without threshold-dependent dynamics, illustrated by the positive effect of nitrate availability on chlorophyll *a* (Fig. 3c; Fig. S8e-f), as well as the between lower and higher trophic levels throughout the food web (Fig. 3g,l,m,s,t,z,aa). In case of omnivory, positive feeding relationships may extend across several trophic levels (Miller *et al.* 2010), such as shown by positive effects of chlorophyll *a* and other zooplankton on euphausiids (Fig. 3l), as well as euphausiids on hake (Buckley & Livingston 1997) (Fig. 3z,aa). The top-down effects are indicated by opposite relationships between adjacent trophic levels, where consumers are positively related to their prey and vice versa (Fig. 3d,h,I,n,u,v,x,ac). In addition, potential competition is illustrated by negative non-trophic interactions, such as shown from cold-water to warm-water euphausiids (Fig. 3q). Interestingly, the negative effects are exclusively threshold-dependent, indicating top-down effects only below or above certain thresholds. Therefore, a negative grazing impact of other zooplankton on primary producers (Mullin 2000) and predation on other zooplankton by mesopelagic and pelagic fish (Ohman & Hsieh 2008) occurred only during periods of low nitrate availability (Fig. 3d,h,i). These conditions primarily exist during El Niño events when diminished upwelling of nutrient rich-water into the SCCS limits primary and secondary production (Chelton *et al.* 1982; Chavez *et al.* 2002). The immediate consequences for pelagic fish are illustrated by significant negative effects from albacore and hake (Fig. 3u,v), but only during periods of high MEI when zooplankton biomass is drastically reduced and food availability limited (Rebstock 2002; Lavaniegos & Ohman 2007). While the top-down effect from albacore can be explained by

predation (Glaser 2010), the negative effect of hake may be due to both predation and competition, especially during early life stages when diet preferences overlap (Buckley & Livingston 1997).

In contrast to the threshold dependent top-down effects, the influence of direct physical forcing is exclusively non-threshold dependent and is optimally described as linear (Fig. 3a,b,e,f,j,k,o,p,r), with the exception of deep-water oxygen which shows a curvilinear relationship to mesopelagic fish (Fig. 3w). Climate effects are illustrated by negative ENSO effect on zooplankton (Fig. 3f) (Rebstock 2002; Lavaniegos & Ohman 2007; Ohman *et al.* 2012), as well as the positive effects of warming (i.e., high PDO and low SOI; Fig. 3o,p) on southern (warm-water) euphausiids (Brinton & Townsend 2003; DiLorenzo & Ohman 2013). Furthermore, we demonstrate positive temperature effect on pelagic fish (Fig. 3r) (Sugihara *et al.*, 2012; Lindegren & Checkley 2013) and positive impacts of nitrate availability (Fig. 3c) and negative effects of density stratification (reduced mixing) on chlorophyll *a* (Fig. 3b) (Mantyla *et al.* 2008). Finally, we show a positive effect of deep-water oxygen on mesopelagic fish (Fig. 3w), likely caused by increased habitat availability and reduced predator-prey overlap (Koslow *et al.*, 2011, 2013, 2014) and a positive effect of sea surface height (i.e., a proxy for the strength of passive advection by the southward flowing California current) on northern (cold-water) euphausiids (Fig. 3j) (Brinton & Townsend 2003).

The separate trophic level models show a good fit to data, being able to accurately recreate the long-term dynamics, as well as inter-annual fluctuations (Fig. S9). Likewise, the hindcast simulations, using the coupled food web model where the internal dynamics (i.e., trophic

interactions) are forced entirely by the external covariates, are able to represent the historical food web dynamics (Fig. 4). However, note that some of the variability is less well represented, especially for higher trophic levels, such as the overestimation of small pelagic fish in the first five years of the hindcast simulations (Fig. 4e). This is due to the coupled structure of the food web model where potential deviations in lower trophic levels, in this case the slight overestimation in both zooplankton and cold-water euphausiids (Fig. 4b,c), propagate through the food web, thereby increasing the uncertainty of predictions at higher trophic levels. In addition, higher trophic levels are not constrained by as many external covariates as the lower trophic levels. Nevertheless, the observed values were within the 95% confidence intervals for all trophic levels. Finally, TGAMs proved significantly better than regular GAMs, as demonstrated by lower genuine CVs (Table 1). However, a regular GAM showed lower gCVs for mesopelagic fish but displayed an insignificant interaction (with hake) and lower explained deviance (65.7%). We therefore used the TGAM formulation, including a significant threshold dependent effect of hake. In addition, the alternative hake model formulation, including pelagic fish biomass as a potential threshold variable, did not show threshold-dependent relationships between prey and predator (Table S4; Figure S10). Since the alternative model resulted in a considerably lower deviance explained (57.2%) compared to the original model using the PDO as a threshold variable (78.9%) we kept the original model. Standard diagnostics of model residuals were satisfactory for all trophic-levels (Figure S11).

The El Niño simulations show a generally strong negative effect on the biota (Fig. 5), particularly for lower trophic levels where chlorophyll *a*, other zooplankton and cold-water euphausiids demonstrate depressed biomasses at about 20-50% of their equilibrium levels,

regardless whether occurring during the negative or positive phase of the PDO. In contrast, higher trophic levels, pelagic and predatory fish (i.e., Pacific hake), respond less negatively to the El Niño event if occurring during the negative phase of the PDO, while during the positive phase of the PDO the biomasses (or abundances) are depressed to about 55% and 30% of their equilibrium levels, respectively. Mesopelagic fish and warm-water euphausiids show moderately, or markedly, positive responses to the El Niño event, particularly during the negative phase of the PDO. However, for euphausiids the magnitude of this increase should be understood in the context of the relatively lower biomass of warm-water euphausiids (Brinton & Townsend 2003). In the second scenario, assessing the effect of exploitation on the commercially important small pelagic fishery, the total pelagic SSB responds drastically to increasing exploitation during unfavorable conditions (Fig. 6), with a minimum SSB at ~25% of the respective equilibrium level at  $F=0.6 \text{ y}^{-1}$ . During favorable conditions the total SSB declines at a more moderate rate with increasing exploitation and demonstrates a higher minimum SSB amounting to ~55% of the respective equilibrium level at  $F=0.6 \text{ y}^{-1}$ .

## Discussion

The identification of dominant modes of ecosystem regulation and the degree to which these may vary in space and time and across ecosystem types, including terrestrial and aquatic ecosystems, represent a long-studied field in ecology (Power 1992; Strong 1992; Polis *et al.*, 2000; Schmitz *et al.*, 2000; Worm & Myers 2003; Strong & Frank 2010; Boyce *et al.*, 2015). On the basis of positive correlations between adjacent trophic levels, a number of large and highly productive marine ecosystems across the North Atlantic and North Pacific, including the California Current,



are considered to be bottom-up driven (Ware & Thompson 2005; Frank *et al.*, 2007; Boyce *et al.*, 2015). Our generalized food web model, using non-linear threshold regressions and a long-term data set spanning six decades, also supports strong bottom-up forcing in the SCCS. This highlights the important regulatory role of nutrient and prey availability, where increased supplies of nitrate (i.e., caused by southern transport of nutrient-rich waters upwelled further north (Chelton *et al.* 1982)) lead to higher primary and secondary production, as well as high abundance of pelagic fish and upper-trophic level predators in the area (Chelton *et al.* 1982; Chavez *et al.* 2003; Mantyla *et al.* 2008), including marine birds and mammals (Melin *et al.*, 2012; Sydeman *et al.* 2015). These resource-driven processes were found to be largely non-threshold dependent. This result implies that bottom-up effects are ever-present and provide a strong baseline regulation of food web dynamics in the SCCS, regardless of highly variable climate conditions. While bottom-up effects on various species or trophic levels in the Northeast Pacific have previously been established (Chavez *et al.* 2003; Ware & Thompson 2005; Sydeman *et al.* 2009), evidence of top-down control has been shown primarily at higher latitudes (Litzow & Ciannelli 2007; Hunt *et al.*, 2011; Boyce *et al.*, 2015), as well as in nearshore and intertidal ecosystems (Paine 1980; Estes *et al.* 1998). Our results support these findings by showing also moderate top-down effects, but interacting with stronger bottom-up forcing throughout the food web. Interestingly, the negative effects are exclusively threshold-dependent, indicating top-down effects only below or above certain thresholds. These thresholds generally correspond to situations when positive bottom-up effects are weakened due to resource limitation, or unfavorable climate conditions. These conditions primarily exist during El Niño events when diminished upwelling of nutrient rich-water into the SCCS limits primary and secondary production (Chelton *et al.* 1982; Chavez *et al.* 2002).

Furthermore, climate-mediated changes in the spatio-temporal overlap between predators and prey may affect the strength of top-down effects. Hence, the negative effect of hake on pelagic fish, as well as albacore on hake, may partly be due to increasing spatial overlap, especially during El Niño events when hake extends its distribution range northward (Agostini *et al.* 2008). Likewise, increased vertical overlap between hake and mesopelagic fish may explain the negative predation effect detected during low oxygen conditions when the mid-water habitat of mesopelagic fish is compressed (Koslow *et al.* 2011, Netburn & Koslow 2015) due to a shoaling of the hypoxic boundary (Bograd *et al.* 2008). Similarly, a fishing effect on hake was found significant only during the negative phase of the PDO. This may be due to lower abundances and a contracted (southerly) distribution range, resulting from stronger equatorward flow by the California current (Agostini *et al.*, 2008), which may increase the vulnerability to fishing. Note that since major changes in hake management (e.g., the transition to a joint Canada-US assessment in 1997; Stewart & Forrest 2011) do not coincide with transitions in the PDO, changes in fishing regulations are unlikely to explain this effect. Although previous studies suggest a marginal effect of hake predation on euphausiids (Mullin & Conversi 1987; Tanasichuk 1999), we found a negative effect on euphausiids occurring only during high chlorophyll *a*. Whether this may be explained by a concentration of hake in the southern area of its distribution range during periods of limited poleward flow (Agostini *et al.* 2008) and high productivity is unclear. Furthermore, whether sharks, billfishes, marine birds and mammals (that were not included in this analysis) can exert a significant regulatory top-down effect on lower trophic levels is unclear. While previous studies demonstrate the importance of bottom-up forcing regulating sea bird populations (Sydeman *et al.*, 2015; Melin *et al.*, 2012), high consumption rates may buffer their relatively low biomasses (Field *et al.*, 2006; Barlow *et al.*,

2008). Hence, these other predators could at least locally (i.e., in the vicinity of bird colonies) and/or seasonally (i.e., during feeding migrations of these highly mobile and wide ranging species) affect the dynamics of their fish and zooplankton prey in the SCCS.

In addition to bottom-up and top-down effects, our model demonstrates pronounced direct physical forcing (Checkley & Barth 2009). These effects are exclusively non-threshold dependent and are illustrated by a suite of interlinked hydrographic processes ranging from regional climate forcing to local impacts acting through temperature, oxygen, upwelling and patterns of transport and advection. This demonstrates the importance of climate and especially alongshore transport on community composition in the SCCS. Depending on the strength and direction of the California Current (as well as the poleward flowing counter current) species with either southern or northern affinities are being advected from, or into the area (Brinton & Townsend 2003; DiLorenzo & Ohman 2013; Koslow *et al.* 2014). This applies also to marine birds where community composition has been shown to shift between cold-water species that dive in pursuit of prey and warm-water species that plunge dive and feed at the surface (Hyrenbach & Veit 2003). In general, we found a stronger influence of direct climate forcing at the base of the food web compared to upper trophic levels where the relative importance of trophic interactions is greater. However, the trophic interactions provide important indirect pathways channelling climate effects from lower trophic levels (Stenseth *et al.* 2002), as well as propagating stochastic and climate-induced variability up the food web, thereby increasing the uncertainty of model predictions at higher trophic levels.

By integrating bottom-up, top-down and direct physical effects our model framework allows for scenario explorations regarding the effect of El Niño events and its potential phase dependence with the PDO (Verdon & Franks 2006). Our simulations show a drastic reduction in biomass (or abundance) across multiple trophic levels during El Niño. The marked decline in lower trophic levels is similar during the negative and positive phase of the PDO and results from weaker bottom-up forcing and increased top-down effects during periods of reduced nutrient supply (Fig. S12). In contrast, the response to El Niño events at higher trophic levels is less pronounced during a negative PDO. In case of pelagic fish this is due to slightly higher biomass of prey (other zooplankton and euphausiids) and considerably lower abundance of predators (hake) when simulated under a negative compared to a positive phase of the PDO (Fig. S13). The lower hake abundance is caused by the negative fishing effect and a lack of positive foraging effects under a negative PDO. In contrast to the other trophic levels, showing a negative response to El Niño, the positive effect on mesopelagic fish reflects a combination of increasing deep-water oxygen and hypothesized reduced predator-prey overlap together with increased northward transport of warm-water fishes by the northward flowing counter current (Koslow *et al.* 2014). Likewise, the positive effect on warm-water euphausiids may be explained by a northward shift in distribution due to increased poleward flow and advection (Brinton & Townsend 2003; Di Lorenzo and Ohman 2013).

As a complement to bottom-up and top-down regulation, wasp-waist control, in which mid-trophic levels may exert both top-down and bottom-up control on their prey and predators, respectively (Rice 1995; Cury *et al.*, 2000), and oscillating trophic control, in which an ecosystem may shift between bottom-up and top-down regulation (Litzow & Ciannelli 2007; Hunt *et al.* 2011), represent additional explanations for understanding ecosystem regulation. In

this study, we found bottom-up control to be the primary mode of ecosystem regulation in the SCCS (Ware & Thompson 2005; Lindegren *et al.* 2016). However, our results indicate also an alternative mode of regulation represented by combined bottom-up and top-down forcing, hence analogous to wasp-waist dynamics, but occurring across multiple trophic levels and only during periods of limiting resources. The shifts in regulation are caused by changes in ocean-atmosphere forcing and are triggered by highly variable climate conditions, such as El Niño, hence analogous to oscillating trophic control (Hunt *et al.*, 2011). Similar climate-mediated shifts between bottom-up and top-down control have also been shown to occur in terrestrial ecosystems, primarily as a response to increased temperature (Hoekman 2010; Rodriguez-Castañeda 2013). The observed shifts in the SCCS do not seem to represent persistent alterations between alternative ecosystem states (i.e., “regime shifts”), but transient events momentarily increasing the relative importance of top-down effects as bottom-up forcing is weakened due to decreasing nutrient concentrations and prey availability. Following these short-lived perturbations the SCCS has been shown to rebound to previous conditions by rapidly regaining primary and secondary production (Rebstock 2001, Ohman *et al.* 2012). In addition to providing a deeper understanding of the roles and relative importance of bottom-up and top-down forces under variable climate conditions, our model simulations highlight important management considerations. Such management concerns are illustrated by an increased sensitivity of the commercially important small pelagic fishery to exploitation during El Niño events, when food availability is limited and predation pressure (natural mortality) is higher. Hence, a holistic ecosystem-based management approach (McLeod & Leslie 2009) accounting for climate-mediated changes in the strength and relative importance of bottom-up and top-down forcing is therefore needed to ensure a sustainable use of marine living resources in the SCCS and beyond.

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666

## 667 **Supporting Information legends**

668 **Table S1.** Biotic and abiotic variables used during model fitting.

669 **Table S2.** Summary statistics of GAM explaining mixed-layer nitrate concentrations and  
670 chlorophyll a.

671 **Table S3.** Summary statistics of the Chl a TGAM when fitted to only observed data from  
672 1984 onwards.

673 **Table S4.** Summary statistics of the hake TGAM when introducing small pelagic fish  
674 spawning stock biomass (SSB) as a threshold variable.

675 **Figure S1.** Map of the study area and the California Cooperative Oceanic Fisheries  
676 Investigations (CalCOFI) long-term monitoring program.

677 **Figure S2.** Partial smooth plots for the GAM explaining variability in mixed-layer nitrate  
678 concentrations.

679 **Figure S3.** Partial smooth plots for the GAM explaining variability in mixed-layer  
680 Chlorophyll a concentrations.

681 **Figure S4.** Observed vs predicted mixed layer nitrate concentrations during years with  
682 a negative PDO.

683 **Figure S5.** Comparison of ichthyoplankton abundance indices and available stock  
684 assessment estimates of spawning stock biomass of sardine and hake.

685 **Figure S6.** A single stochastic model run showing the effect on the biota of an  
686 introduced El Niño event.

687 **Figure S7.** The estimated thresholds and time-series of threshold variables for the final  
688 TGAMs.

689 **Figure S8.** Partial smooth plots for the final TGAM for Chl a when fitted on the entire  
690 time-series and when fitted on observed values only from 1984 onwards.

691 **Figure S89** Observed and fitted food web dynamics based on the final models.

692 **Figure S10.** Summary plot showing the alternative hake TGAM if introducing the  
693 spawning stock biomass of small pelagic fish as a threshold variable.

694 **Figure S11.** Residual diagnostic plots for the final models.

695 **Figure S12.** The response of Chl a when including or significantly limiting the threshold  
696 dependent top-down effect of zooplankton grazing during a simulated El Niño event.

697 **Figure S13.** Simulated food web responses to a negative and positive phase of the  
698 PDO.

699 **Appendix S1.** Additional sensitivity tests for trophic-level models.

**Table 1.** Summary statistics showing the intercept with p-value, the estimated threshold, the deviance explained (DEV in %), the genuine cross-validation score (gCV), comparing TGAM and GAMs, the number of observations (N), as well as smooth term statistics for each TGAM. Significant terms “above”, “below or equal to”, or without the estimated threshold are denoted by  $>$ ,  $\leq$  and  $--$ , respectively. (edf, estimated degrees of freedom for the model smooth terms where  $\text{edf} > 1$  indicates a nonlinear relationship).

Response	Intercept	P-value	Threshold ( $\Phi$ )	DEV (%)	gCV <sub>TGAM/GAM</sub>	N
Chl $\alpha$	0.24	<0.001	0.498	77.9	0.027/0.029	58
Other Zooplankton	3.03	<0.001	0.735	57.0	0.211/0.235	52
Euphausiid (cool)	1.73	<0.001	0.279	69.3	0.242/0.243	56
Euphausiid (warm)	0.42	<0.001	-0.225	63.0	0.233/0.249	55
Pelagic fish	13.6	<0.001	0.371	68.1	0.512 /0.535	37
Mesopelagic fish	2.36	<0.001	1.517	73.0	0.143/0.125	45
Pacific hake	3.51	<0.001	-0.251	78.9	0.817/1.12	42

Response	Threshold	Predictor	edf	F	P-value
Chl $\alpha$	---	SST	1.00	14.1	<0.001
	---	Density	1.00	50.2	<0.001
	---	[NO <sub>3</sub> ]	1.96	36.9	<0.001
	[NO <sub>3</sub> ] $\leq \Phi$	Other Zooplankton	1.00	6.36	0.015
Other Zooplankton	---	PDO	1.85	10.4	<0.001
	---	MEI	1.58	7.60	0.001
	---	Chl $\alpha$	1.00	6.10	0.017
	[NO <sub>3</sub> ] $\leq \Phi$	Pelagic fish	1.27	4.96	0.011
	[NO <sub>3</sub> ] $\leq \Phi$	Mesopelagic fish	1.00	7.35	0.009
Euphausiid (cool)	---	Dynamic height	1.00	19.6	<0.001
	---	Sverdrup transport	1.00	8.82	0.005
	---	Chl $\alpha$	1.64	4.00	0.025
	Chl $\alpha \leq \Phi$	Other Zooplankton	1.00	8.55	0.005

729		Chl $\alpha > \Phi$	Pacific hake	1.91	14.2	<0.001
730	Euphausiid (warm)	---	PDO	1.02	8.60	<0.001
731		---	SOI	1.00	10.60	0.002
732		PDO $> \Phi$	Euphausiid (cool)	1.72	10.41	0.002
733	Pelagic fish	---	SST	1.00	8.23	0.007
734		---	Euphausiid cool	1.00	12.62	0.001
735		MEI $\leq \Phi$	Other Zooplankton	1.00	13.0	<0.001
736		MEI $> \Phi$	Pacific hake	1.00	10.7	0.003
737		MEI $> \Phi$	Albacore	1.00	9.86	0.004
738	Mesopelagic fish	---	[O <sub>2</sub> ] (200-400m)	1.99	42.2	<0.001
739		[O <sub>2</sub> ] $\leq \Phi$	Pacific hake	1.79	5.42	0.008
740	Pacific hake	---	Mesopelagic	1.86	13.7	<0.001
741		PDO $> \Phi$	Euphausiid (cool)	1.78	11.5	<0.001
742		PDO $> \Phi$	Euphausiid (warm)	1.56	7.10	0.003
743		PDO $> \Phi$	Pelagic fish	1.00	43.1	<0.001
744		PDO $> \Phi$	Albacore	1.00	8.98	0.005
745		PDO $\leq \Phi$	F	1.00	11.54	0.002
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**Figure 1.** A conceptual representation of the dominant modes of ecosystem regulation within a simplified four-level marine food web. (a) Bottom-up regulation is typically characterized by a positive relationship between trophic levels where an increase in primary producers leads to increases in higher trophic levels. (b) Top-down regulation is represented by negative relationship between adjacent trophic levels, usually characterized by alternating abundance trends in response to a decline in top-predators. (c) Wasp-waist regulation occurs when mid-trophic levels (e.g., small planktivorous fish) exert both top-down control on their prey (zooplankton) and bottom-up control on their predators. (d) Finally, our results indicate an alternative mode of regulation represented by strong and persistent bottom-up forcing interacting with weaker top-down forcing, but only above or below certain thresholds, here associated with climate-related changes in ENSO. This mode of regulation is related to wasp-waist and oscillating trophic control, occurring when the modes of ecosystem regulation shift between bottom-up and top-down control (usually as a result of rapid changes in the environment). However, in the mode of regulation presented here the shifts are between strict bottom-up forcing and a combination of both bottom-up and top-down control. (This figure is inspired and partly redrawn from Cury *et al.*, 2003).

**Figure 2.** A schematic representation of the effects of climate, fishing and trophic interactions in the generalized SCCS food web model, consisting of Pacific hake, mesopelagic fish, small pelagic fish, euphausiids, i.e., divided into a cold (C) and warm (W) water assemblage, mesozooplankton and primary producers. (Note that the top-predator albacore tuna (within dotted rectangle) is treated as an external covariate). Blue and red arrows indicate threshold-dependent interactions above and below an estimated threshold, respectively (Fig. S6). The

numbers associated with each arrow correspond to a particular covariate used as threshold variable, identified by the same number in superscript. The black arrows indicate non-threshold dependent effects. Although interactions may range from linear to non-linear, we have indicated generally positive (+) and negative (-) interactions.

**Figure 3.** Partial effect plots from the final set of trophic level models showing the relationship between abiotic and biotic variables and chlorophyll a (a-d), other mesozooplankton (e-i), euphausiids divided into a cold- (j-n) and warm water (o-q) assemblage, small pelagic fish (r-v), mesopelagic fish (w-x) and Pacific hake (y-ad). Variable names are shown in the bottom-right corner of each panel. The associated x-axis show the range of values within which the relationships are fitted. Light blue and red lines indicate threshold-dependent interactions above and below the estimated thresholds, respectively (Fig. S7), while black lines indicate non-threshold dependent effects. Dashed lines show the 95% confidence intervals of each partial effect. (See Appendix S1 for additional sensitivity tests of partial effects and threshold estimates).

**Figure 4.** Observed (circles) and hindcasted dynamics of chlorophyll a (A), other mesozooplankton (B), cold- and warm-water euphausiids (C-D), small pelagic fish (E), mesopelagic fish (F) and Pacific hake (G). The simulations are initiated with observed population estimates in 1966 and simulated until 2010 based on observed external covariates only. Grey lines show 95% confidence intervals. (See Fig. S9 for model fits).

**Figure 5.** Simulated effects of a major El Niño event on chlorophyll a (C), other mesozooplankton (Z), cold- and warm-water euphausiids (Ec, Ew), small pelagic fish (P), mesopelagic fish (M) and hake (H). The effects are quantified as the change in (non-log) biomass (or abundance) relative to a baseline level during a negative (white) or a positive phase of the PDO (gray). (A value of 1 indicates no change). The additional y-axis applies to warm-water euphausiids demonstrating a considerably larger relative change in biomass in response to El Niño.

**Figure 6.** Impact of increasing exploitation, i.e., fishing mortality (F), on small pelagic fish during periods of low (black) and high (gray) MEI. The effect is quantified as the change in total biomass relative to a respective equilibrium level (i.e., 0.77 and 0.44 Million metric tons at  $F=0$ ) when forced by mean climate conditions occurring below (black) and above (gray) the MEI threshold (Fig. S7i,j), respectively. Solid and dashed lines show the mean and 95% confidence intervals after 1000 random simulations.

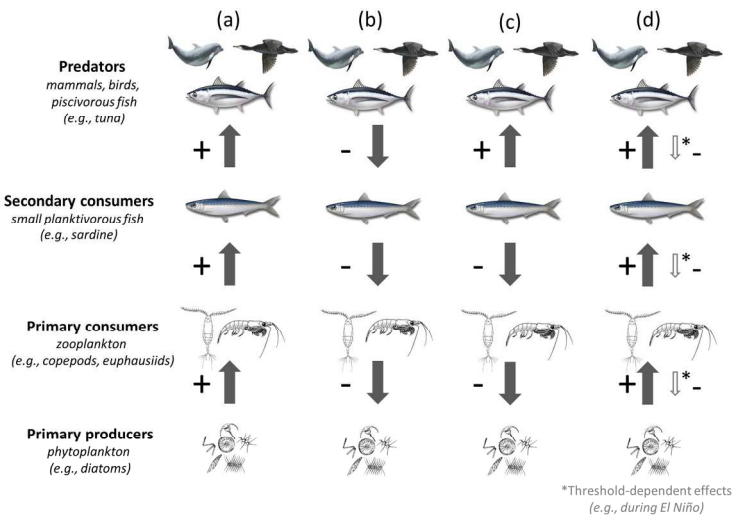


Fig 1

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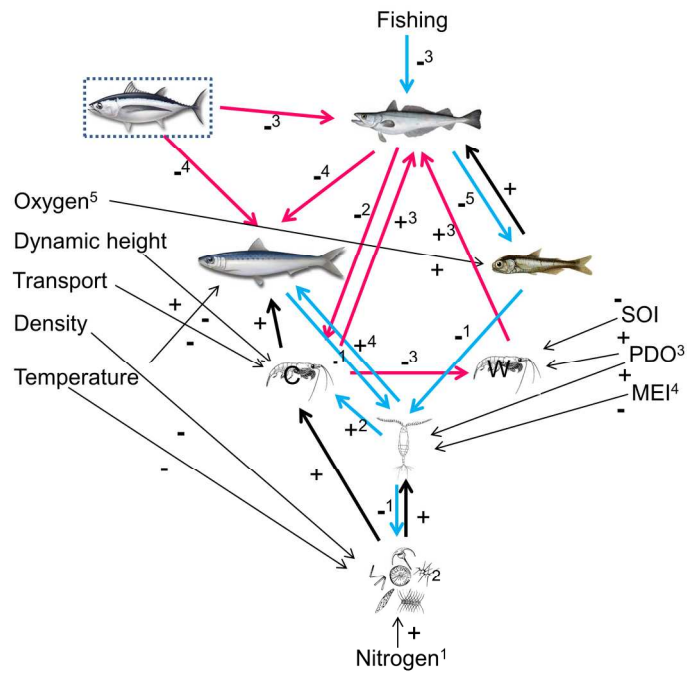


Fig 2

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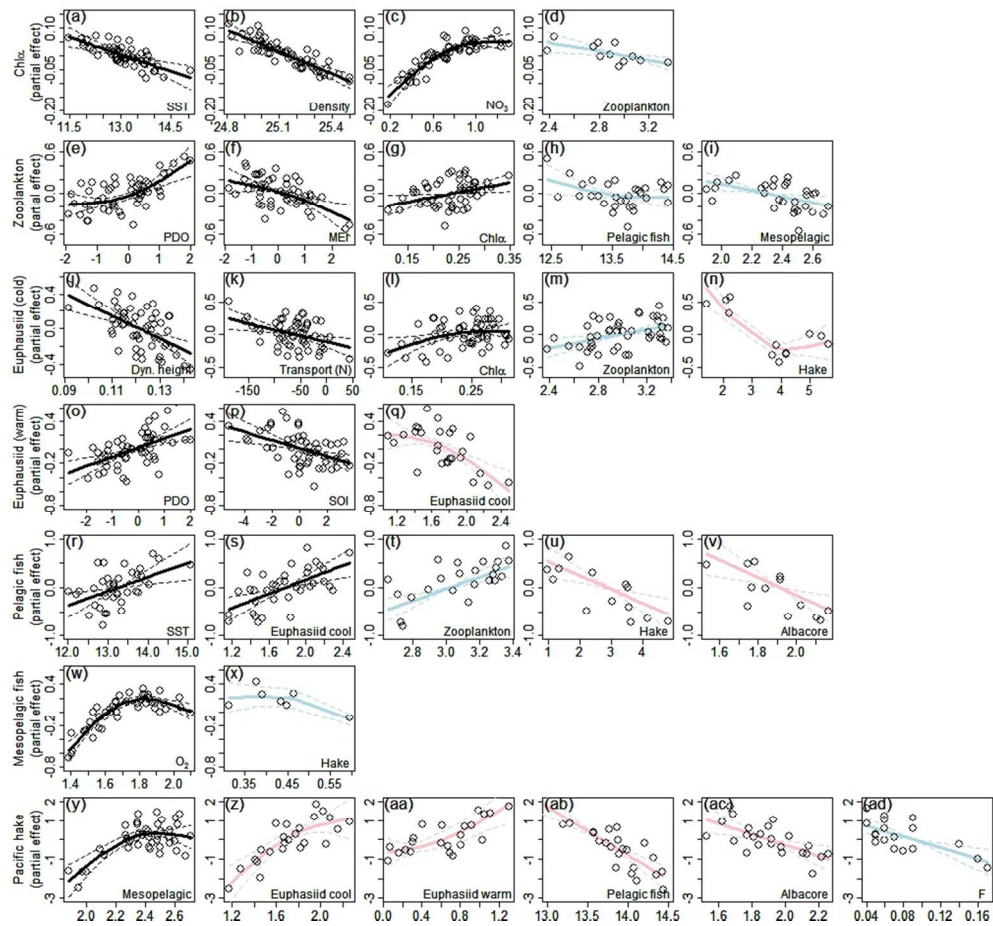
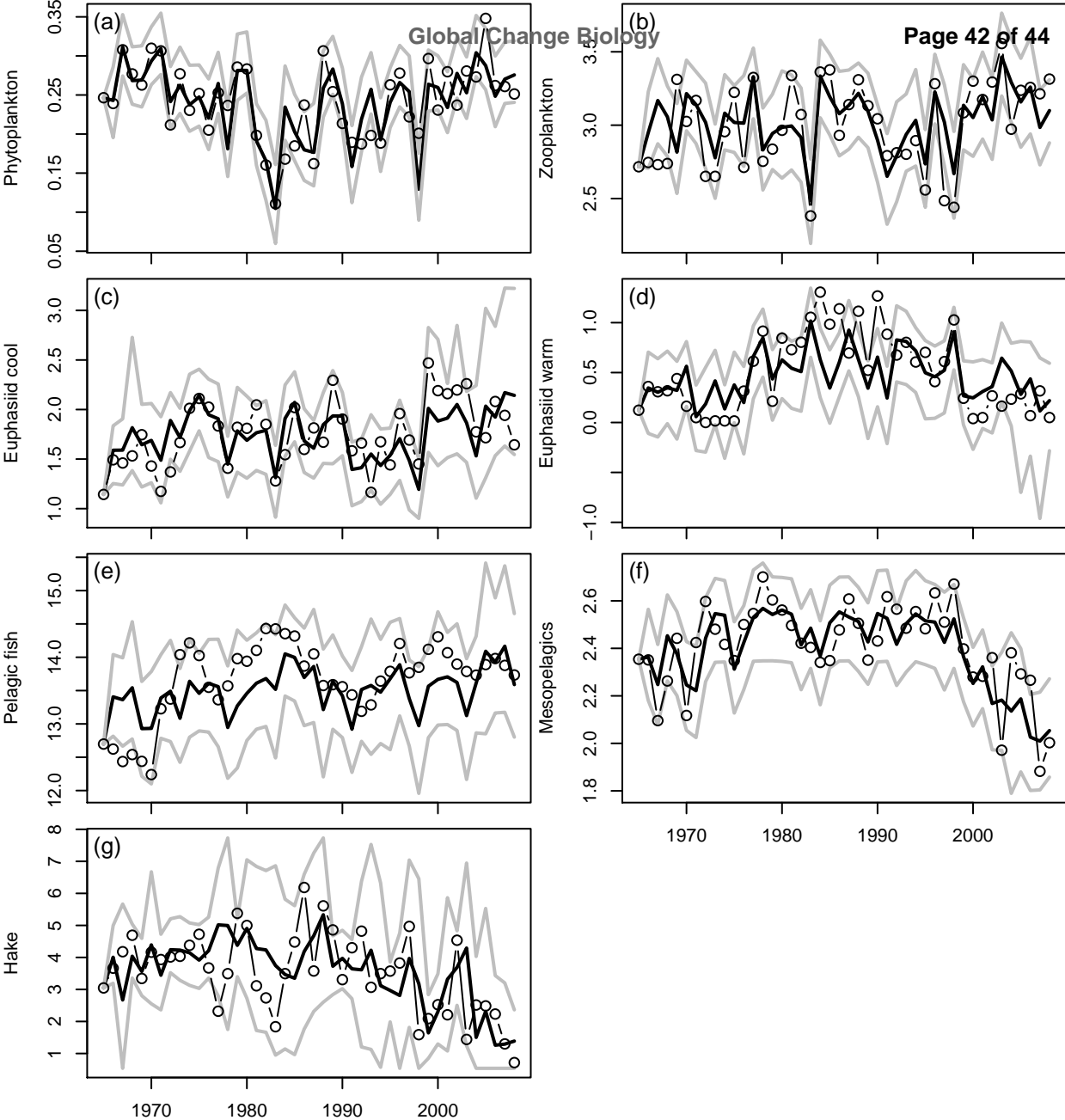


Fig 3

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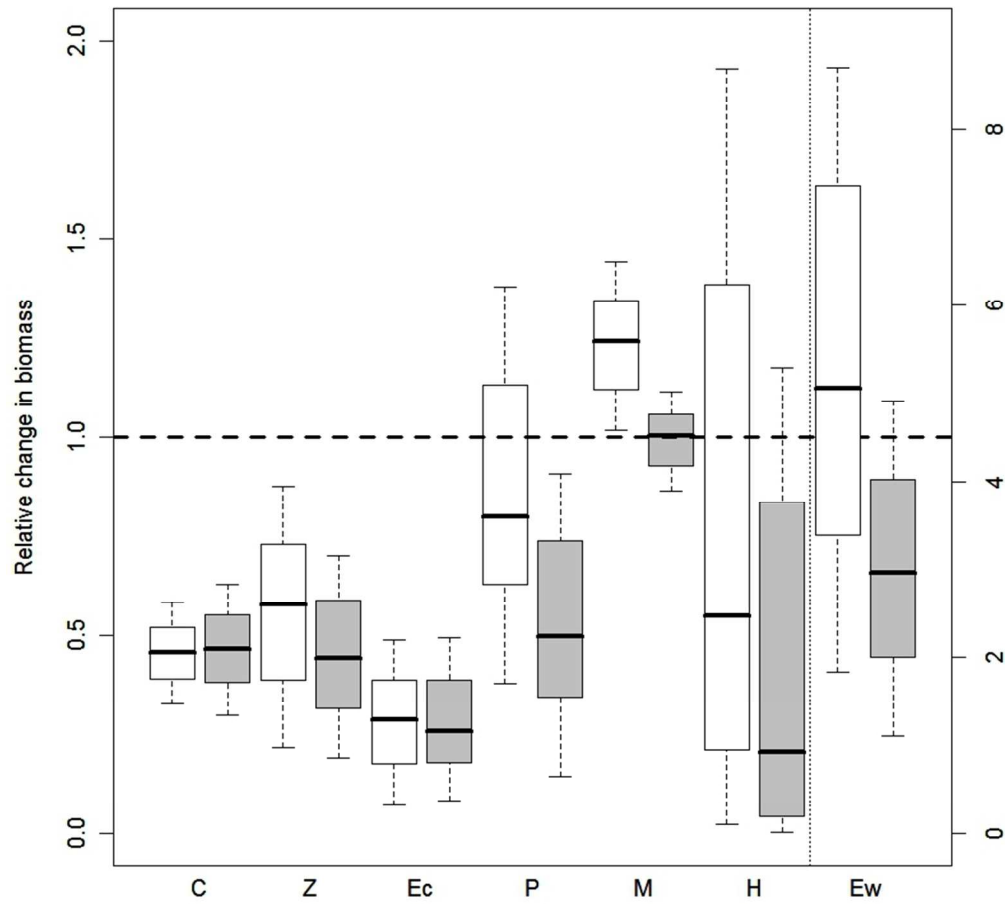


Fig 5

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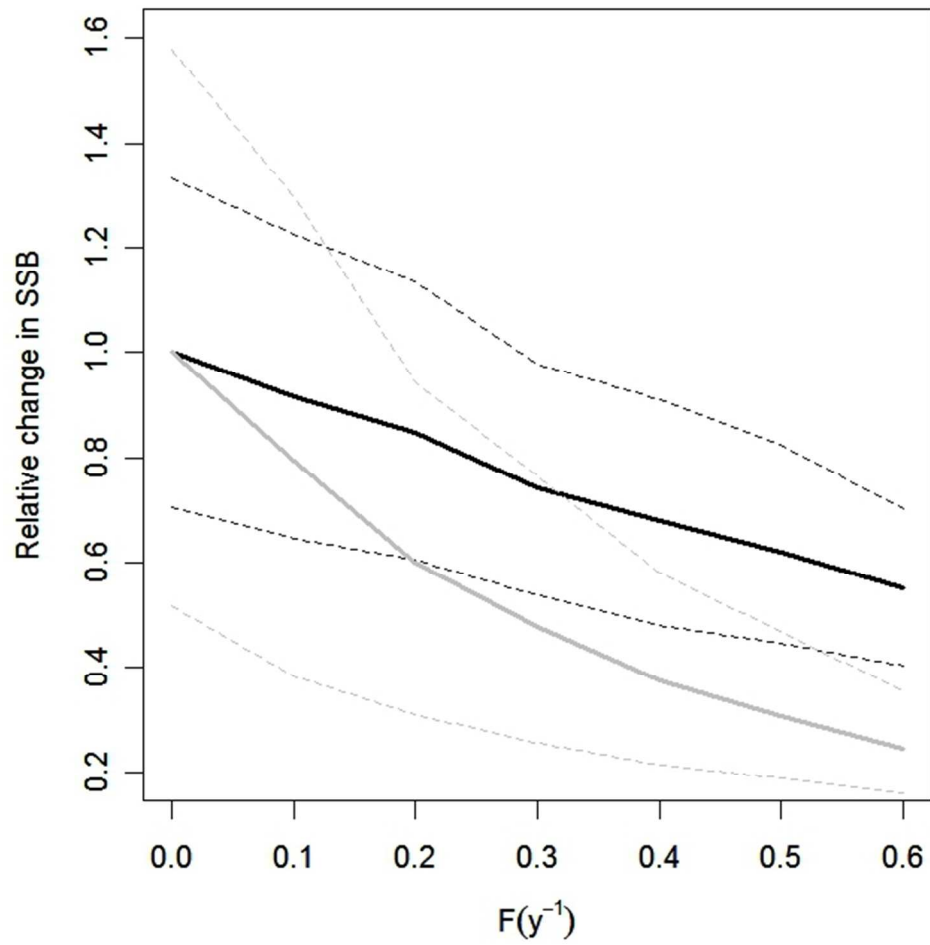


Fig 6

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